

# 1 **Mate choice in a changing world**

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## 11 **ABSTRACT**

12 Human activities by altering environmental conditions are influencing the mate choice of animals.

13 This is by impacts on: (1) the production and expression of traits evaluated by mate choosers; (2)

14 the transmission of information about potential mates to choosers; (3) the reception and processing

15 of the information by choosers; and (4) the final mate choice. Here, I first discuss how these four

16 stages of the mate-choice process can be altered by environmental change, and how these

17 alterations, in turn, can influence individuals, populations, and communities. Much evidence exists

18 for human-induced environmental changes influencing mate choice, but the consequences for the

19 fitness of courters and choosers are less well known, and even less is known about the impact on

20 population dynamics, species interactions and community composition. More evidence exists for

21 altered mate-choice systems influencing interspecific matings and thereby community composition

22 and biodiversity. I then consider whether plastic adjustments and evolutionary changes can rescue

23 adaptive mate-choice systems, and reflect on the possibility of non-adaptive mate-choice systems

24 becoming less maladaptive under environmental change. Much evidence exists for plastic

25 adjustments of mate-choice systems, but whether these are adaptive is seldom known, as is the

26 contribution of genetic changes. Finally, I contemplate the possibility of mate-choice systems  
 27 rescuing populations from decline in changing environments. I explain how this is context  
 28 dependent with both positive and negative outcomes possible. In summary, while much evidence  
 29 exists for human-induced environmental changes influencing mate-choice systems, less is known  
 30 about the consequences for ecological and evolutionary processes. Considering the importance that  
 31 mate choice plays in determining individual fitness and population viability, the effects of  
 32 environmental change on mate-choice systems should be considered in studies on the ecological  
 33 and evolutionary consequences of human disturbances to habitats.

34

35 *Key words:* communication, courtship, environmental change, female choice, male–male  
 36 competition, multimodal, multiple cues, ornamentation, sexual selection, signal interactions.

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38 CONTENTS

39 Contents.....2  
 40 I. Introduction ..... 3  
 41 II. Dependence of mate choice on environmental conditions ..... 6  
 42 III. Influence of environmental change on mate-choice cues..... 7  
 43 (1) Expression of cues ..... 7  
 44 (2) Transmission of information ..... 8  
 45 (3) Interactions among cues ..... 9  
 46 IV. Influence of environmental change on mate assessment and choice ..... 10  
 47 (1) Evaluation of cues..... 10  
 48 (2) Shifting among cues..... 11  
 49 (3) Mate choice ..... 13  
 50 V. Consequences of altered mate-choice systems ..... 13  
 51 (1) Individual level ..... 14  
 52 (2) Population level ..... 18  
 53 (3) Community level ..... 21  
 54 VI. Can adaptive mate-choice systems be rescued?..... 23  
 55 (1) Plastic adjustments..... 23  
 56 (2) Genetic changes ..... 24  
 57 VII. Can mate choice rescue populations?..... 25  
 58 VIII. Open questions ..... 27  
 59 IX. Conclusions..... 28  
 60 X. Acknowledgements..... 29  
 61 XI. References..... 30

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## 63 **I. INTRODUCTION**

64 Environments around the world are changing rapidly because of human activities. This is  
65 influencing the mate choice of animals, as both the expression of the assessed traits and the choice  
66 behaviour of the chooser depend on environmental conditions (Rosenthal, 2017; Rosenthal &  
67 Stuart-Fox, 2012). Traffic noise, for instance, is masking the courtship songs of birds, while  
68 pollution with synthetic hormones is reducing the motivation of fishes to make careful mate choices  
69 (Wong & Candolin, 2015). The mate-choice process can be divided into four pre-mating stages that  
70 are sensitive to environmental conditions: (1) the production and expression of the traits evaluated  
71 by mate choosers; (2) the transmission of information about potential mates through the  
72 surroundings to the choosers; (3) the reception and processing of the information by the choosers;  
73 and (4) the final mate choice. Changes in environmental conditions that alter the amount or  
74 reliability of information emitted, or the transmission of the information through the medium, can  
75 alter the information that reaches the chooser. Correspondingly, environmental changes that  
76 influence the ability of choosers to receive and process the information, or to act appropriately, can  
77 alter their ability to make informed mate choices.

78 The traits assessed during mate choice can take a variety of forms; they can be visual, auditory,  
79 chemical, tactile, or electrical. They can be unimodal and involve only one sensory modality, or be  
80 multimodal and combine multiple sensory modalities, such as both visual and auditory channels  
81 (Partan & Marler, 2005). Some traits are intentional signals, which have been moulded by sexual  
82 selection to attract mates (Andersson, 1994). Others are cues that have evolved in another context  
83 but come to be used as indicators of some aspects of mate quality. An example of the latter is body  
84 size, which is often used as an indicator of body condition and, supposedly, of phenotypic and  
85 genetic quality. The assessed traits can indicate direct benefits to choosers, such as material  
86 resources or parenting ability, or indirect genetic benefits that either improve offspring viability –

87 through the inheritance of ‘good genes’ or ‘compatible genes’ – or enhance their attractiveness,  
88 through the inheritance of the attractive trait (the Fisherian process) (Andersson, 1994).  
89 Alternatively, the traits can be uninformative arbitrary traits that have evolved because courters take  
90 advantage of pre-existing sensory biases in choosers (Endler & Basolo, 1998). These traits may not  
91 reflect any fitness benefits to choosers, and could even reduce their fitness. Deceptive traits with a  
92 negative impact on choosers can evolve when the interests of the two sexes differ (sexual conflict),  
93 as courters may attempt to maximise their individual fitness at a cost to choosers (Arnqvist &  
94 Rowe, 2005; Holland & Rice, 1998; Ryan & Rand, 1993). This can result in a co-evolutionary arms  
95 race between the sexes where individuals attempt to maximise their own fitness by manipulating the  
96 opposite sex.

97 Many animals assess multiple traits during mate choice. This can increase the amount and reliability  
98 of information received, facilitate detection, or allow informed mate choices under different  
99 conditions, such as under various social settings, distances, or times of the day. Alternatively,  
100 preferences for multiple cues can be the remnants of past selection and not convey any benefits to  
101 choosers under present conditions. The preferences could even be disadvantageous if courters  
102 exploit sensory biases in choosers (Bro-Jorgensen, 2010; Candolin, 2003; Hebets & Papaj, 2005;  
103 Moller & Pomiankowski, 1993; Uy & Safran, 2013).

104 Assessing multiple traits can be a strength in changing environments if the different traits reflect  
105 fitness benefits. It can allow choosers to switch among traits depending on their ease of assessment  
106 and reliability. However, the benefit depends on the assessed traits conveying the same information  
107 about mate quality (back-up cues) (Partan, 2017). If the traits convey different information  
108 (multiple messages), switching among them can result in the loss of information. Female three-  
109 spined stickleback (*Gasterosteus aculeatus*), for example, lose information about mate quality when  
110 they switch from a predominant use of visual signals to an increased use of olfactory ones in algal-

111 turbid water (Heuschele *et al.*, 2009). Moreover, the assessment of multiple cues can increase the  
112 probability that at least some of the assessed cues become less reliable indicators of mate quality.  
113 How animals respond to human-induced environmental changes depends on their reaction norms  
114 for plastic responses, and the possibility of genetic changes. Reaction norms for responses may not  
115 be adaptive when animals encounter novel conditions that they have not encountered in their recent  
116 evolutionary history (Candolin & Wong, 2012; Sih, Ferrari & Harris, 2011; Tuomainen &  
117 Candolin, 2011). Genetic changes require, in turn, the presence of genetic variation in the direction  
118 of selection (Barrett & Hendry, 2012). Such changes take time to appear as they occur across  
119 generations. Many animals may consequently not be able to adjust and adapt their mate-choice  
120 system to rapid human-induced environmental changes. On the other hand, maladaptive mate-  
121 choice systems may become less maladaptive under altered conditions, if courters are less able to  
122 exploit pre-existing sensory biases in choosers, or to override the mate choices of choosers.  
123 Here, I discuss how human-induced environmental changes can influence the mate-choice process,  
124 and the consequences that alterations can have for individuals, populations and communities. I  
125 begin by discussing the sensitivity of mate choice to environmental change, and explain how  
126 alterations in extrinsic factors and intrinsic properties of individuals can influence the different  
127 stages of mate choice. I then move on to consider the consequences that alterations in the different  
128 stages of mate choice can have for the fitness of individuals and the dynamics of populations and  
129 communities. Next, I discuss whether adaptive mate-choice systems can be rescued by plastic  
130 adjustments and evolutionary changes, and whether maladaptive mate-choice systems could even  
131 become less maladaptive. Finally, I consider whether mate-choice systems rescue or endanger  
132 populations in human-disturbed environments. I concentrate on human-induced environmental  
133 changes, such as habitat degradation, pollution, climate change, harvesting, and species  
134 introduction. These create particularly challenging conditions for organisms because of the rate and

135 scale at which they occur. For simplicity, I often refer to assessed traits as cues although they can be  
136 intentional signals.

137

## 138 **II. DEPENDENCE OF MATE CHOICE ON ENVIRONMENTAL CONDITIONS**

139 Mate-choice systems are the result of a coevolutionary process between choosers and courtiers  
140 (Endler, 1992; Endler & Basolo, 1998; Rosenthal, 2017). Choosers have evolved to assess traits that  
141 are easy to evaluate and reflect mate qualities under prevailing conditions, such as parenting ability  
142 or breeding value for viability, while courtiers have evolved to invest in traits that attract mates, such  
143 as ornaments and courtship displays. Individuals can be both choosers and courtiers, but usually one  
144 of the roles dominates, with females generally being choosier and males more likely to court.

145 The costs and benefits of the traits used in mate choice depend on environmental conditions. For  
146 instance, the cost of conspicuous courtship displays depends on the abundance of predators using  
147 visual cues to detect prey, while the benefit depends on visibility. Similarly, the costs and benefits  
148 of mate choice depend on the environment: the cost of searching for mates may depend on predator  
149 abundance, while the benefit may depend on the ability of the chosen mate to provide for and  
150 protect the offspring under local conditions, as well as on its breeding value, which varies  
151 depending on how well suited to local conditions the individual is.

152 This environment dependence of the costs and benefits of mate-choice traits implies that changes in  
153 the environment can alter the adaptive value of the traits used to attract mates and to find and select  
154 a mate (Bro-Jorgensen, 2010; Candolin & Wong, 2012; Partan, 2013; Rosenthal & Stuart-Fox,  
155 2012; van der Sluijs *et al.*, 2011). Human-induced environmental changes are particularly likely to  
156 compromise their value, as the changes are often rapid and result in novel conditions that the  
157 species has not encountered during its recent evolutionary past (Sih *et al.*, 2011; Tuomainen &  
158 Candolin, 2011). Traffic noise, for instance, which has increased rapidly around the world, has

159 altered the background noise of the songs of birds. This is hampering the ability of birds to evaluate  
160 the quality of the songs of potential mates (Francis & Barber, 2013).

161 Below, I discuss how the different stages of the mate-choice process can be affected by  
162 environmental change (Fig. 1). There are two main pathways through which this can occur, through  
163 effects on (1) the expression of the traits used in mate attraction and mate choice, such as courtship  
164 displays and mate preferences, and (2) the adaptedness of the traits, such as signal efficacy and the  
165 benefit of mate preferences.

166

### 167 **III. INFLUENCE OF ENVIRONMENTAL CHANGE ON MATE-CHOICE CUES**

#### 168 **(1) Expression of cues**

169 Environmental change can influence the traits of courters by altering (1) the external surroundings,  
170 or (2) the intrinsic properties of courters (Fig. 1). Altered external surroundings can change the  
171 amount of resources that can be invested into mate attraction, or the benefit of the investment. Wolf  
172 spiders (*Rabidosa rabida*), for instance, reduce their use of visual displays when visibility is poor  
173 and rely instead more heavily on seismic signals (Wilgers & Hebets, 2011). Likewise, altered  
174 population characteristics, such as density, operational sex ratio, and social context, can influence  
175 investment into mate attraction. This is by changing the intensity of competition for mates, or the  
176 encounter rate with potential mates (Emlen & Oring, 1977; Kokko & Rankin, 2006; Shuster, 2009).  
177 For example, female giant pandas (*Ailuropoda melanoleuca*) adjust their investment into signals of  
178 reproductive status depending on how human activities alter the presence of other females (Owen *et*  
179 *al.*, 2016).

180 Changes in intrinsic properties of courters, such as body condition or physiological processes, can  
181 similarly influence their investment into mate attraction (Cotton, Fowler & Pomiankowski, 2004;  
182 Hill, 2011). For instance, the exposure of guppy (*Poecilia reticulata*) males to the endocrine-

183 disrupting chemical 17 $\beta$ -trenbolone – a hormonal growth promotant used in livestock production –  
184 causes them to perform less courtship towards females (Bertram *et al.*, 2015).

185 Altered expression of mate-choice cues can be adaptive or maladaptive. Adaptive adjustments may  
186 occur when courters respond to changes in the costs and benefits of expressing the cues. For  
187 example, reduced investment into mate attraction can be adaptive when resource availability  
188 declines, as it may free up resources for investment into more-pressing activities, such as foraging  
189 or predator avoidance (Fig. 2). However, when animals encounter novel conditions that they have  
190 not experienced in their recent evolutionary past, adaptive reaction norms may not exist and the  
191 responses may also be mal-adaptive (Fig. 2). For instance, man-made chemicals, such as  
192 pharmaceuticals and pesticides, can induce changes in signals that are not correlated with changes  
193 in mate quality (Arellano-Aguilar & Garcia, 2008; Bertram *et al.*, 2015; Soffker & Tyler, 2012). On  
194 the other hand, if signals and cues are quantitative and can only change in one direction, such as  
195 enlarging or shrinking, then changes may, by chance alone, be in the right direction for half the  
196 time.

197 Courters can also take advantage of human-induced environmental changes. For instance, satin  
198 bowerbird males (*Ptilonorhynchus violaceus*) increase their attractiveness to females by decorating  
199 their bowers with blue man-made objects that they collect from the surroundings, such as blue  
200 bottle tops (Borgia, 1985). Similarly, traits may gain new functions and serve as exaptations that  
201 improve mating success (Gould & Vrba, 1982). For example, body size may become a new  
202 indicator of parenting ability if resources decline and the difference in body size among individuals  
203 increases, as the difference may then be a better indicator of the ability of the potential mates to  
204 provide for the offspring under the altered conditions.

205

206 **(2) Transmission of information**



207 For the information content of signals and cues to reach the chooser, the information has to be  
208 transmitted through a medium, such as air, water, soil, rock, or vegetation. The efficiency of this  
209 transmission can be altered by anthropogenic disturbances (Endler, 1992). Urban noise, for  
210 instance, masks acoustic signals (Francis & Barber, 2013; Gil & Brumm, 2014; Shannon *et al.*,  
211 2016), while altered forest composition influences the contrast between ornaments and the visual  
212 background (Delhey & Peters, 2017; Endler & Thery, 1996).

213 Some species are able to adjust their signals and cues to altered transmission. Many songbirds, for  
214 example, sing at higher frequencies when traffic noise masks their normal vocalisations (Gil &  
215 Brumm, 2014). Other species shift the timing of singing towards the night when noise levels are  
216 lower (Fuller, Warren & Gaston, 2007), or shorten their calls, or pause singing more often (Orci,  
217 Petroczki & Barta, 2016). These adjustments can be plastic responses to the altered conditions, or  
218 evolutionary changes, but their relative contribution is usually unknown.

219

### 220 **(3) Interactions among cues**

221 When multiple cues are used in mate assessment, interactions among them can occur (Candolin,  
222 2003; Hasson, 1991). Alterations in one cue can then amplify, modify or dampen the influence of  
223 environmental change on other cues, and thus have a disproportionately large impact on information  
224 transmission. For instance, a reduction in ornament size in response to chemical pollution can  
225 decrease the visibility of courtship displays (Saaristo *et al.*, 2018). Correspondingly, a reduction in  
226 courtship activity, for instance because of an increased abundance of predators, can diminish the  
227 visibility of ornaments. An example is the water boatman (*Sigara falleni*) that exposes its foreleg  
228 palae to females during courtship. The size of the palae indicates the condition of the male, and a  
229 decrease in courtship activity – because of an increased abundance of predators – reduces the  
230 exposure of the palae to females and, hence, the transmission of the information about male  
231 condition (Candolin, 2005).

232

233 **IV. INFLUENCE OF ENVIRONMENTAL CHANGE ON MATE ASSESSMENT AND**  
234 **CHOICE**

235 **(1) Evaluation of cues**

236 Changes in the environment can influence mate assessment by altering (1) the amount and quality  
237 of information that reaches mate choosers, (2) the ability of choosers to receive and process the  
238 information, (3) the mate preferences of the choosers, and (4) the investment of choosers into mate  
239 evaluation.

240 Changes in the amount and quality of information that reaches choosers can alter mate-encounter  
241 rate, or the effort choosers spend on locating and evaluating courters (Endler, 1992). For instance,  
242 increased habitat complexity hampers the ability of female three-spined stickleback visually to  
243 detect courting males, which reduces the number of males they evaluate (Heuschele, Salminen &  
244 Candolin, 2012). Changed environmental conditions also can influence the ability of choosers to  
245 discriminate among courters, by altering the difference among them in signal quality, or the  
246 transmission of information about courters to choosers.

247 Changes in the ability of choosers to receive and process the information transmitted can similarly  
248 influence mate evaluation (Boughman, 2002; Endler, 1992; Endler & Basolo, 1998). For instance,  
249 chemical pollution can influence the physiological processes needed to assess mates (Saaristo *et al.*,  
250 2018). Distractions also can interfere with the ability of choosers to concentrate on mate evaluation.  
251 Traffic noise, for example, distracts female field crickets (*Gryllus bimaculatus*), which reduces their  
252 ability to locate males based on their courtship song (Schmidt, Morrison & Kunc, 2014).

253 Mate preferences are also sensitive to changes in the number of courters detected and their  
254 perceived quality. For instance, choosers may inspect fewer mates closely if these are perceived to  
255 be of poor condition. Likewise, changes in the intrinsic state of choosers, for example because of  
256 chemical pollution, can reduce the motivation of choosers to evaluate courters carefully.

257 Whether altered mate evaluation is adaptive or maladaptive depends on how the costs and benefits  
258 of mate evaluation change (Cotton, Small & Pomiankowski, 2006; Jennions & Petrie, 1997;  
259 Rodriguez, Rebar & Fowler-Finn, 2013). A reduction in choosiness may be beneficial when the  
260 predation risk cost of mate evaluation increases, or environmental conditions deteriorate and  
261 relatively more time and energy needs to be allocated to body maintenance. For example, female  
262 pronghorns (*Antilocapra americana*) decrease their mate-sampling effort during hot and dry  
263 summers when they are in poor condition, as they then have less energy available for mate sampling  
264 (Byers, Byers & Dunn, 2006). On the other hand, when species encounter novel conditions that they  
265 are not adapted to, alterations in mate evaluation may be maladaptive. Evolutionary traps, in  
266 particular, when preferences that were adaptive in the past environment become maladaptive in the  
267 new environment, are likely to result in maladaptive mate evaluation (Schlaepfer, Runge &  
268 Sherman, 2002). An infamous example is male jewel beetles (*Julodimorpha bakewelli*) that are  
269 attracted to beer bottles because their texture resembles that of females (Gwynne & Rentz, 1983).

270

## 271 **(2) Shifting among cues**

272 When some cues become difficult to evaluate, or unreliable indicators of mate quality, choosers  
273 may benefit from plastically shifting their attention to other cues that are easier to evaluate, or more  
274 reliable indicators of quality. For instance, female painted goby (*Pomatoschistus pictus*) switch  
275 from a dominant use of acoustic signals to an increased use of visual signals when noise levels  
276 increase (de Jong *et al.*, 2018). Such shifts among sensory modalities may be common when cues in  
277 one sensory modality become difficult to evaluate (Bro-Jorgensen, 2010; Heuschele *et al.*, 2009;  
278 Munoz & Blumstein, 2012; Partan, 2013).

279 Whether shifts among cues improve mate evaluation depends on the reliability of the cues, as well  
280 as on their overlap in information content, i.e. if they are back-up cues or multiple messages (Ay,  
281 Flack & Krakauer, 2007; Partan, 2013). When cues indicate different qualities, shifting among them

282 can result in the loss of information, as discussed in Section I. Moreover, when one cue needs to  
283 exceed a threshold level before other cues are evaluated (sequential evaluation), changes in the first  
284 cue can influence the evaluation of subsequent cues. For instance, female wolf spiders (*Schizocosa*  
285 *uetzi*) pay less attention to male visual ornaments if vibrational signals are attenuated (Hebets,  
286 2005). Similarly, if different signals are assessed at different distances, a reduction in the efficacy of  
287 long-distance signals can decrease the number of mates inspected for close-range signals. This can  
288 result in more-random mate choices if the long-distance signals are used to attract mates while the  
289 close-range signals give information about mate quality. For example, the attractiveness of long-  
290 distance signals in the field cricket (*Gryllus integer*) influences the assessment of close-range  
291 signals, which give additional information about mate quality (Leonard & Hedrick, 2010). Thus,  
292 noise that hampers the assessment of long-distance signals in crickets, such as traffic noise, can  
293 reduce the ability of females to focus their evaluation on the most attractive males. This can  
294 increase the costs of mate evaluation in terms of time, energy and predation risk, or result in more  
295 maladaptive choices.

296 Organisms may lack reaction norms for adaptively shifting among cues when encountering novel  
297 conditions. For example, females of the European treefrog (*Hyla arborea*) are not able to decrease  
298 their use of acoustic signals in favour of visual signals under traffic noise, although both acoustic  
299 and visual signals are used in mate evaluation (Troianowski, Melot & Lengagne, 2014). Populations  
300 from variable environments are more likely to be able to shift among cues than populations from  
301 more-stable environments, as they are more prone to have evolved preferences for cues that convey  
302 the same information under the variable conditions in their past environment (Bro-Jorgensen, 2010).  
303 Populations from stable environments, on the other hand, are more likely to use cues that reflect  
304 unique aspects of mate quality (multiple messages), as the use of unnecessary cues can be costly  
305 (Johnstone, 1996).

306 An alternative to shifting among cues is to take in new cues. However, perceptual restrictions may  
307 prevent the adoption of new cues, and their evolution may be too slow to rescue mating systems in  
308 rapidly changing environments.

309

### 310 **(3) Mate choice**

311 Changes in the environment that influence mate evaluation, preferences, or choosiness can  
312 influence mate choice. For instance, female palmate newts (*Lissotriton helveticus*) change their  
313 mate choice when exposed to waterborne chemicals from exotic eucalyptus plantations. This is  
314 because they lose their ability to distinguish among males based on cues positively correlated with  
315 the male's immune response (Iglesias-Carrasco *et al.*, 2017).

316 If the environmental change impairs the ability of individuals to recognise conspecifics, the  
317 frequency of heterospecific matings may increase. For example, the exposure of the freshwater fish  
318 *Cyprinella venusta* and its introduced congener *C. lutrensis* to the endocrine-disrupting chemical  
319 bisphenol A (BPA) increases hybridization between the two species (Ward & Blum, 2012). This is  
320 because the chemical impairs species recognition by reducing the ornamentation of the males, as  
321 well as by lowering female mate-choice thresholds.

322 Evolutionary traps are particularly likely to cause maladaptive mate choices (Schlaepfer *et al.*,  
323 2002). Species, or objects, that were not encountered in the evolutionary history of the species may  
324 emit cues that resemble those of mates and that consequently are attractive. A classic example is the  
325 earlier mentioned example of Jewel beetles mating with beer bottles (Gwynne & Rentz, 1983).

326

## 327 **V. CONSEQUENCES OF ALTERED MATE-CHOICE SYSTEMS**

328 Alterations of mate-choice systems in human-disturbed habitats can influence the survival and  
329 reproductive success of individuals. For instance, the clearance of sheltering vegetation can increase  
330 predation risk for courtiers, while noise that hampers the detection of mates can reduce reproductive

331 success of choosers. Such changes can impinge on population dynamics. Altered population  
332 dynamics can, in turn, influence species interactions, such as consumer–resource and competitive  
333 interactions, and, hence, have further consequences for community structure. Alterations to  
334 communities can again impact on ecological processes, such as the flow of energy and material  
335 through the ecosystem. Over longer time spans, mate-choice traits may become adapted to novel  
336 conditions through genetic evolutionary processes. Such changes can, in turn, influence the  
337 evolution of correlated traits and, hence, contribute to speciation. Thus, alterations of mate-choice  
338 systems can have far-reaching consequences for populations, communities and ecosystems.  
339 Below, I discuss the consequences that altered mate-choice systems can have for the different levels  
340 of ecological organisation, from individuals to populations to communities. I explain when and how  
341 mate-choice systems can be adjusted, and possibly adapted, to rapid environmental changes, and  
342 whether mate choice generally aids or impedes adaptation to human-disturbed habitats. Little  
343 research has been conducted on these questions and I therefore concentrate on what is expected  
344 based on theory. I pinpoint the most imminent gaps in our knowledge, to encourage more research  
345 into this important research field.

346

#### 347 **(1) Individual level**

348 The influence of an altered mate-choice system on the fitness of courters and choosers – their  
349 survival and reproductive success – depends on how the costs and benefits of their traits change  
350 when the environment changes. Costs are the allocation of time, energy and resources to the traits at  
351 the expense of other fitness-related traits such as growth, as well as increased risk of premature  
352 death. Benefits are increased mating success in terms of number and/or quality of mates gained  
353 (Halfwerk *et al.*, 2018). Human-induced environmental changes that alter these costs and benefits  
354 can alter the number and quality of offspring produced. However, while much evidence exists of  
355 animals altering their mate-choice traits in response to human-induced environmental change, less

356 is known about the impact on individual fitness. Most responses appear to be maladaptive and  
357 increase the cost of attracting and choosing mates, or result in less-careful mate choice, but the  
358 impact on the number and quality of offspring produced is usually unknown (Candolin, Salesto &  
359 Evers, 2007; Delhey & Peters, 2017; Radford, Kerridge & Simpson, 2014; Rosenthal & Stuart-Fox,  
360 2012). A recent example of a negative effect of an altered mate-choice system on individual fitness  
361 is female three-spined sticklebacks choosing a mate in anthropogenically eutrophied habitats:  
362 females are more likely to choose a male that sires offspring of low viability when visibility is poor  
363 because of algal blooms (Candolin, Tukiainen & Bertell, 2016).

364 The reliability of mate-choice cues as indicators of fitness benefits can decrease when signalling  
365 systems are disrupted. Reliability depends on the transmitted information correlating with the direct  
366 and indirect benefits that the courters can provide, such as parenting ability or heritable viability.  
367 This correlation can be disrupted by changes in (1) the expression of the mate-choice cues, (2) the  
368 benefits the courters can offer, or (3) the transmission and reception of the information about  
369 courters (Fig. 3). Disruptions are particularly likely in human-disturbed environments, as the  
370 conditions often differ from those under which the traits have evolved. Light pollution, for instance,  
371 interferes with the transmission of the glow of females of the common glow-worm (*Lampyris*  
372 *noctiluca*). This hampers the ability of males to judge female fecundity, as fecundity correlates with  
373 female size, which correlates with glow brightness (Bird & Parker, 2014; Hopkins *et al.*, 2015).

374 Genotype-by-environment interactions (GEIs) have recently gained much attention in the context of  
375 cue reliability (Bussiere *et al.*, 2008; Higginson & Reader, 2009; Hunt & Hosken, 2014; Ingleby,  
376 Hunt & Hosken, 2010; Sgro & Hoffmann, 2004). This is because the correlation between cues and  
377 genetic composition can be disrupted when genotypes differ in their response to environmental  
378 change. For example, the reliability of the cuticular hydrocarbons of *Drosophila simulans* as  
379 signals of heritable attractiveness is reduced when diet and temperature change between generations  
380 (Ingleby, Hunt & Hosken, 2013).

381 The impact of an altered mate-choice system on fitness can differ between courters and choosers, as  
382 the importance of careful mate choice usually differs between the sexes. Courters, which typically  
383 are males, usually benefit from a higher mating rate than choosers, which typically are females.  
384 This is because males generally have a higher potential reproductive rate than females (Clutton-  
385 Brock & Parker, 1992). Choosers benefit instead from more-careful mate choice, because of their  
386 lower potential reproductive rate. Thus, the variation in mating success is often higher among  
387 courters than among choosers (as a few courters may gain most matings). Environmental change  
388 that alters the possibility of careful mate choice can then have a larger impact on the variation in  
389 mating success among courters than among choosers. For instance, relaxed mate choice may  
390 increase the mating success of poor competitors, while the losers may be the most attractive  
391 courters with a high mating success in the undisturbed habitat. Choosers may be more equally  
392 affected, but instead experience a reduction in the quality of mates they acquire.

393 The impact of an altered mate-choice system on fitness is also contingent on the adaptedness of the  
394 system. When the system was adaptive before conditions changed, from the choosers' point of  
395 view, choosers may suffer fitness reductions if the system changes. On the other hand, if the system  
396 was maladaptive before the environment changed, because courters manipulated choosers to make  
397 sub-optimal choices, or overrode their choices through forced copulations, choosers could benefit  
398 from environmental change; the change could decrease the ability of courters to manipulate  
399 choosers or their success in forced copulations. The impact on courters depends again on whether  
400 the courters were successful competitors for mates in the undisturbed environment; successful  
401 competitors may experience fitness losses, while poor competitors could improve their fitness. In  
402 support of disturbed environments relaxing sexual conflict – and thereby its negative effect on  
403 offspring production – *Drosophila melanogaster* produce fitter offspring when individuals are  
404 displaced from their naturally selected optimum, i.e. when they are less well adapted to local  
405 conditions (Long, Agrawal & Rowe, 2012). Similarly, seed beetles (*Callosobruchus maculatus*)



406 display less intralocus sexual conflict when exposed to stressful temperatures (Berger *et al.*, 2014).  
407 However, the degree to which mate-choice systems are maladaptive under undisturbed conditions is  
408 poorly known, and even less is known about the impact of disruptions to maladaptive systems on  
409 individual fitness.

410 The influence of environmental change on the adaptedness of mate choice can also vary depending  
411 on the indicator value of the assessed traits. Traits that reflect direct benefits or heritable viability  
412 (through the inheritance of ‘good genes’ or ‘compatible genes’) are probably more sensitive to  
413 changes in individual performance than traits that reflect heritable attractiveness (Fisherian traits).  
414 For instance, an increased abundance of carotenoid-rich food may reduce the value of red  
415 ornaments as indicators of foraging ability and, hence, their reliability as signals of parenting ability  
416 or heritable viability (Svensson & Wong, 2011). The value of red ornaments as indicators of  
417 heritable attractiveness may not be affected, as pre-existing sensory biases of choosers are not  
418 altered. On the other hand, if the efficacy of the signals is altered, such as the contrast of the red  
419 ornaments against the background, all forms of signals may be affected. Moreover, if the traits are  
420 deceptive traits, such as sensory traps that mimic stimuli that individuals respond to in other  
421 contexts (Christy, 1995), then reduced efficacy could benefit choosers. Correspondingly, if the  
422 efficacy of deceptive traits improves, the fitness of the choosers could decrease.

423 Individuals may attempt to prevent negative effects of environmental change on their mating  
424 success by adjusting their traits to the changes. Most responses to human-induced rapid  
425 environmental changes appear to be plastic responses, and less evidence exists for evolutionary  
426 changes (Hendry, Farrugia & Kinnison, 2008). The plastic adjustments can be adaptive and improve  
427 reproductive success. For example, female lark buntings (*Calamospiza melanocorys*) plastically  
428 adjust their choice of ornamented males to climate conditions, which increases their probability of  
429 choosing a male with a high nesting success under prevailing conditions (Chaine & Lyon, 2008).  
430 However, when organisms encounter novel conditions – which is often the case in human-disturbed

431 habitats – the responses may instead be maladaptive and reduce fitness. For example, male great tits  
432 (*Parus major*), which adjust their songs to anthropogenic noise in order to reduce its masking  
433 impact, suffer from reduced female fertility and fidelity, as the altered song is not preferred by  
434 females (Halfwerk *et al.*, 2011).

435 An altered mate-choice system can result in mating attempts being directed towards heterospecifics  
436 or non-living objects. This is the case if the environmental change reduces the ability of individuals  
437 to recognise conspecifics, or to distinguish them from unsuitable targets. Such changes can  
438 significantly increase the costs of mate choice. For example, males of the frog *Rana draytonii* clasp  
439 juveniles of the invasive American bullfrog (*Rana catesbeiana*) in the belief that these are large  
440 conspecific females (D'Amore, Kirby & Hemingway, 2009). This wastes time and energy and can  
441 increase predation risk, as bullfrogs are voracious, opportunistic predators. Similarly, when two  
442 related species come into secondary contact, they may emit cues that attract the other species. This  
443 can result in no viable offspring, or in hybrids with low viability.

444 In general, our knowledge of the effects of altered mate-choice systems on individual fitness is still  
445 poor (Candolin & Wong, 2012; Read, Jones & Radford, 2014). This is because of the challenge of  
446 investigating fitness consequences, as both offspring and grand-offspring production should ideally  
447 be measured. Below, I discuss the potential consequences that altered individual fitness can have for  
448 population dynamics.

449

## 450 **(2) Population level**

451 Changes to mate-choice systems that alter the number and viability of offspring produced could  
452 influence population dynamics (Fig. 4). However, the ultimate impact on populations can be  
453 difficult to discern, as density-dependent mortality can dampen the effect (Holman & Kokko, 2013),  
454 and as interactions with other changes, such as in life-history traits, can further influence the impact  
455 of altered mate-choice systems (McLean *et al.*, 2016).

456 Changes in the number of individuals reproducing can influence offspring production. This is  
457 particularly the case if the number of females reproducing is altered. For instance, light pollution  
458 that reduces the visibility of the glow of female glow-worms hampers the ability of males to locate  
459 females, which can leave many females unmated (Bird & Parker, 2014). Similarly, evolutionary  
460 traps that cause misdirected mating attempts can reduce the number of individuals reproducing  
461 (Robertson, Rehage & Sih, 2013). Changes in sex ratio or age distribution can also influence the  
462 size of the reproducing population. For example, a sex ratio skewed towards females because of  
463 endocrine-disrupting chemicals can leave many females unmated. Likewise, increased mortality  
464 among young individuals – for instance because of increased predation risk – can reduce the size of  
465 the reproducing population.

466 The individuals that reproduce can, in turn, have their offspring production altered. However, a  
467 reduced number of offspring may not decrease population growth rate if the offspring are highly  
468 viable, as a higher proportion of the offspring could survive until adulthood. Correspondingly, an  
469 increased number of offspring produced can still cause a decline in population growth rate, if the  
470 offspring are poorly adapted to the novel conditions and suffer high mortality.

471 Declining recruitment can combine with an Allee effect (lower mate encounter rate in smaller  
472 populations) and further shrink the population (Kokko & Brooks, 2003). This can, in the worst-case  
473 scenario, result in the extinction of the species. An anecdotal example is the Irish elk (*Megaloceros*  
474 *giganteus*), whose extinction has been attributed to an increased cost of developing and carrying  
475 large antlers in an increasingly hostile environment (Moen, Pastor & Cohen, 1999; Worman &  
476 Kimbrell, 2008). Another potential example is the high extinction rate among sexually dichromatic  
477 birds (Doherty *et al.*, 2003). However, the relative contribution of sexual selection to extinction is  
478 unclear, as the assumed costs mostly affect males. A reduction in the number of males reproducing  
479 may not influence population dynamics, if a few males can fertilise most females. Rather than being

480 the sole cause of population decline, increased costs of sexually selected traits may combine with  
481 other factors to influence population dynamics.

482 Disturbed mate choice can alter also the spatial and temporal distribution of populations. For  
483 instance, individuals may abandon areas where noise reduces the efficacy of mate-choice signals  
484 (Francis & Barber, 2013). Examples are declines in songbird diversity in areas with high levels of  
485 anthropogenic noise (Proppe, Sturdy & St Clair, 2013).

486 A reduced cost of mate-choice traits can, in turn, improve population viability. For instance,  
487 declining predator abundance can reduce the cost of mate sampling, which can increase both  
488 survival and the possibility of careful mate choice. Sexually selected traits are often costly and  
489 opposed by natural selection for improved viability and fecundity (Kokko & Brooks, 2003). Thus, a  
490 reduced use of them can enhance population viability. However, the impact depends also on  
491 whether the costs or benefits of the traits dominated in the undisturbed environment, and how these  
492 change in the disturbed environment (Candolin & Heuschele, 2008). If sexual conflict dominated in  
493 the past, then reduced efficiency of the traits used to manipulate the opposite sex could improve  
494 population viability.

495 Evolutionary processes can change as well in response to altered mate-choice systems. For instance,  
496 hampered mate choice in fishes when rampant algal growth reduces visibility relaxes selection on  
497 sexually selected traits (Candolin, 2009; Candolin & Vlieger, 2013; van der Sluijs *et al.*, 2011).

498 Such changes can result in population divergence, and possibly in speciation, if populations  
499 exposed to different anthropogenic disturbances differentiate in their mate-choice cues and  
500 preferences (Boughman, 2002; Coyne & Orr, 2004; Endler, 1992; Schluter & Price, 1993). The use  
501 of multiple cues can facilitate such differentiation, as populations exposed to different disturbances  
502 can emphasise different cues (Schaefer & Ruxton, 2015; Uy & Safran, 2013; Vortman *et al.*, 2013).

503 In support of this, populations exposed to dissimilar environmental conditions often differentiate in  
504 their sexually selected traits, as observed for barn swallows (*Hirundo rustica*) (Romano *et al.*,

505 2017), flycatchers (*Monarcha castaneiventris*) (Uy, Moyle & Filardi, 2009), and antbirds (Seddon,  
506 Merrill & Tobias, 2008).

507 Changes in population dynamics can, in turn, influence species interactions and, hence, the  
508 community of species.

509

### 510 **(3) Community level**

511 Changes to mate-choice systems that influence the demography and evolution of populations, or the  
512 ability of individuals to differentiate between conspecifics and heterospecifics, can influence  
513 species interactions and thereby the composition of biological communities. Impacts through  
514 interspecific matings have received much attention, while effects through altered population  
515 dynamics are less well studied. One example of an effect through altered population dynamics is a  
516 bird community in New Mexico where species composition changed in response to noise pollution:  
517 birds unable to adjust their vocalisations to noise declined, while those that could adjust increased  
518 (Francis, Ortega & Cruz, 2009). Such changes could cascade through the species community *via*  
519 species interactions and further alter the composition (Kunc, McLaughlin & Schmidt, 2016; Wong  
520 & Candolin, 2015). For instance, the crash of a population of fathead minnows (*Pimephales*  
521 *promelas*) when exposed to a synthetic oestrogen – which disrupted its mate-choice system –  
522 favoured the population growth of its prey, zooplankton, but caused a decline in its predator  
523 population, the lake trout (*Salvelinus namaycush*) (Kidd *et al.*, 2014).

524 Changes in interspecific mating attempts can again influence communities through effects on  
525 offspring production, both within species and through the production of hybrids. When interspecific  
526 mating attempts increase, but result in no viable offspring, the size of the populations may decline.  
527 This may be because of (1) fewer intraspecific matings, (2) the depletion of essential resources,  
528 such as time, energy and nutrients, or (3) increased susceptibility to predators and parasites  
529 (Gröning & Hochkirch, 2008; Kyogoku, 2015). Such costs of interspecific matings can, in turn,

530 promote reproductive character displacement, to reduce the risk of costly matings. This can promote  
531 population differentiation and, possibly contribute to speciation (Cothran, 2015; Kyogoku, 2015;  
532 Pfennig & Pfennig, 2009). Species that are particularly likely to mate with each other because of  
533 disrupted mate-choice systems are species that do not differentiate in other traits than the mate-  
534 choice traits, and, hence, rely on these for species separation (M'Gonigle *et al.*, 2012).

535 When interspecific matings result in viable hybrids, species may merge, or new hybrid lineages may  
536 emerge (Todesco *et al.*, 2016). A classic example is Lake Victoria cichlids that have hybridised into  
537 much fewer species because of reduced visibility in the anthropogenically eutrophied lakes  
538 (Seehausen, Alphen & Witte, 1997). Currently, new contact zones are created among species  
539 because of climate change, as this triggers range shifts. This is promoting hybridisation among  
540 species and altering biodiversity (Chunco, 2014). For instance, the expansion by southern flying  
541 squirrels (*Glaucomys volans*) towards the north has resulted in habitat overlap with the northern  
542 flying squirrel (*G. sabrinus*) and, hence, in hybridisation between the two species (Garroway *et al.*,  
543 2010).

544 Other forms of species interactions are also sensitive to altered mate-choice systems, such as  
545 predator–prey, host–parasite, mutualistic and competitive interactions. Many predators, for instance,  
546 locate their prey based on conspicuous mate-choice traits, such as loud calls or bright colours. One  
547 example is the European perch (*Perca fluviatilis*), which preferentially preys upon colourful,  
548 courting stickleback males (Johnson & Candolin, 2017). Reduced visibility in eutrophied habitats  
549 thus reduces predation rate on these conspicuous males, which can influence the dynamics of both  
550 the predator and the prey. Similarly, changes in mate-searching activity can alter encounters with  
551 parasites and, hence, host–parasite interactions. Moreover, non-indigenous species that invade new  
552 habitats may be mistaken as conspecific rivals and increase aggressive interactions in native  
553 species, by causing misdirected rivalry attacks during male–male (or female–female) competition  
554 for mates (Gröning & Hochkirch, 2008).

555 The opposite direction of events, with altered species interactions influencing mate-choice systems  
556 and, thus, populations and communities, is also plausible, as well as feedbacks between altered  
557 mate-choice systems and species interactions. Invasive species, for instance, can disturb sexual  
558 communication in native species by masking or altering their signals. For instance, the calls of the  
559 invasive American bullfrog (*Lithobates catesbeianus*) cause native Brazilian frogs to modify their  
560 calls (Both & Grant, 2012; Medeiros *et al.*, 2017). Similarly, the invasive cane toad (*Rhinella*  
561 *marina*) causes a native Australian frog (*Limnodynastes convexiusculus*) to reduce its calling  
562 (Bleach *et al.*, 2015). Such changes in mate-choice systems can alter the population dynamics of the  
563 affected species.

## 564

## 565 **VI. CAN ADAPTIVE MATE-CHOICE SYSTEMS BE RESCUED?**

566 When adaptive mate-choice systems are disrupted by human activities, their rescue hinges on  
567 plastic adjustments and evolutionary adaptation of the traits to the novel conditions (Fig. 5).  
568 Whether the rescue succeeds depends on a large number of factors, such as (1) the difference of the  
569 novel environment to earlier encountered conditions, (2) the rate at which the environment changes,  
570 (3) the presence of suitable genetic variation, and (4) the strength of sexual selection (Barrett &  
571 Hendry, 2012; Chevin *et al.*, 2013; Chevin & Lande, 2010). An interaction between plastic  
572 responses and evolutionary processes can occur, with plastic adjustments either facilitating or  
573 hindering evolution (Hendry, 2016; Pfennig *et al.*, 2010). Plasticity facilitates evolution if it exposes  
574 hidden genetic variation to selection, or provides more time for evolution to take place, by  
575 preventing drastic population declines. However, plasticity can also constrain evolution if it buffers  
576 against the disturbance and thereby hides genetic variation (Pfennig *et al.*, 2010; Schlichting &  
577 Wund, 2014) (Fig. 5).

### 578

### 579 **(1) Plastic adjustments**

580 Much evidence exists for plastic adjustments of mate-choice traits to human-induced environmental  
581 changes. Most of the examples discussed herein are probably plastic responses. For instance, birds  
582 adjust plastically their songs to traffic noise (Gil & Brumm, 2014), while fishes adjust their  
583 courtship behaviours, ornaments, and mate preferences to algal blooms and turbidity changes  
584 (Engström-Öst & Candolin, 2007; Tuomainen, Sylvén & Candolin, 2011). Whether the adjustments  
585 are adaptive is, however, usually unknown. Plastic alterations are determined by existing reaction  
586 norms, which have evolved under past environmental conditions and, hence, may not be adaptive  
587 under altered conditions (McNamara *et al.*, 2011; Sih, 2013; Tuomainen & Candolin, 2011). On the  
588 contrary, when conditions differ drastically from the past, the responses are more likely to be  
589 maladaptive (Ghalambor *et al.*, 2007). Adaptive responses may instead occur when altered  
590 conditions are extremes of earlier encountered conditions. Thus, species from fluctuating  
591 environments may be more plastic than species from stable habitats, depending on the predictability  
592 of the environment and the generation time of the species (Gomez-Mestre & Jovani, 2013; Hendry,  
593 2016; Svanbäck, Pineda-Krch & Doebeli, 2009).

594

## 595 **(2) Genetic changes**

596 Populations may be able to evolve mate-choice systems better suited altered conditions. The  
597 probability increases with shorter generation time, larger population size, presence of suitable  
598 genetic variation, and stronger sexual selection (Barrett & Schluter, 2008; Hendry, Gotanda &  
599 Svensson, 2017). However, selection can also promote the evolution of stronger sexual conflict and,  
600 hence, of reproductive load. Little is currently known about the evolution of mate-choice systems in  
601 response to human-induced environmental changes. Much evidence exists for evolution of mate-  
602 choice systems in response to natural environmental changes (Hendry *et al.*, 2008; Svensson &  
603 Gosden, 2007). However, evolution in human-disturbed habitats can be constrained by the lack of  
604 suitable standing genetic variation, as conditions often differ drastically from those in the species'



605 evolutionary past. In addition, the rapidity of human-induced changes may exceed the rate of  
606 evolution.

607 The scarcity of evidence for evolutionary responses to human-induced environmental changes can  
608 also be due to the difficulty of separating plastic and genetic responses in the wild (Merila &  
609 Hendry, 2014; Prokuda & Roff, 2014; van Benthem *et al.*, 2017). One potential example of an  
610 evolutionary response is the sexually selected forehead patch of the collared flycatcher (*Ficedula*  
611 *albicollis*), which has become smaller during a 34-year period of climate change, apparently  
612 because of a trade-off with survival (Evans & Gustafsson, 2017).

613

## 614 **VII. CAN MATE CHOICE RESCUE POPULATIONS?**

615 As discussed earlier, alterations to mate-choice systems can influence population viability by  
616 changing the number and viability of offspring produced. The effects can be either positive or  
617 negative, with negative effects probably dominating in human-disturbed environments, because of  
618 the lack of adaptive reaction norms (Sih *et al.*, 2011; Tuomainen & Candolin, 2011). However, over  
619 time mate-choice systems may evolve and become better adapted to new conditions. Whether this  
620 will rescue the systems, and possibly the populations, depends on how fast the evolutionary changes  
621 occur, whether the good genes or the Fisherian process dominates, and the degree to which sexual  
622 conflict reduces viability. If selection for ‘good genes’ or ‘compatible genes’ dominates, which  
623 select for individuals best adapted to prevailing conditions, the viability of the populations may  
624 improve (Lorch *et al.*, 2003). On the other hand, if the Fisherian process dominates, which selects  
625 for traits that increase attractiveness, but not necessarily viability, the populations may decline.  
626 Whether sexual selection facilitates or hinders adaptation to rapid, human-induced environmental  
627 change is disputed and appears to vary among populations, species, and context (Candolin &  
628 Heuschele, 2008; Holman & Kokko, 2013; Martinez-Ruiz & Knell, 2017). While selection for  
629 ‘good genes’ and ‘compatible genes’ can improve offspring viability, the effect on populations

630 depends also on the number of offspring produced, i.e. on female survival and fecundity. If higher  
631 costs of mate choice lower female fecundity, or increase mortality, or if sexual conflict increases  
632 male harassment and manipulation, fewer offspring may be produced (Arnqvist & Rowe, 2005).  
633 This may not be compensated by higher offspring viability, in which case the population may  
634 decline.

635 The impact of sexual selection on population viability depends also on a range of other factors, such  
636 as (1) life-history strategies, (2) the degree of polygamy, (3) the condition-dependence of sexually  
637 selected traits, (4) population size, (5) inbreeding, and (6) existing genetic variation (Barrett &  
638 Hendry, 2012; Hendry *et al.*, 2017; Lorch *et al.*, 2003; Martinez-Ruiz & Knell, 2017; Plesnar-  
639 Bielak *et al.*, 2012; Winemiller, 1992). Life-history strategies influence the rate of adaptation, as *r*-  
640 selected populations can evolve faster than *K*-selected, because of their larger offspring production  
641 and shorter generation time. Polygamy intensifies, in turn, selection for ‘good genes’ and  
642 ‘compatible genes’, which can accelerate adaptation. Condition dependence of sexually selected  
643 traits can again ensure that the assessed traits reflect viability under prevailing conditions and,  
644 hence, facilitate adaptive mate choice. In addition, larger populations may have larger evolutionary  
645 potential than smaller populations because of higher standing genetic variation and higher  
646 mutational input. In small populations, inbreeding may instead erode genetic variation.

647 On the other hand, if the mate-choice system was maladaptive before the environment changed,  
648 alterations to the system could reduce the cost of mate choice to females and promote population  
649 growth. Environmental change is predicted to decrease sexual conflict, as the proportion of sexually  
650 antagonistic alleles in relation to generally maladaptive alleles is predicted to decrease (Long *et al.*,  
651 2012; Martinez-Ruiz & Knell, 2017). However, the degree to which this reduces the absolute cost  
652 of sexual selection in populations is unclear.

653 Thus, while mate choice may contribute to rescuing populations, the effect depends also on the  
654 impact on female fecundity and survival, and whether the mate-choice system was adaptive or

655 maladaptive before humans altered the environment. A range of factors can influence the process in  
656 the short and in the long term.

657

### 658 **VIII. OPEN QUESTIONS**

659 We have a relatively good understanding of the mechanisms behind effects of environmental  
660 change on mate-choice systems, i.e. on mate attraction and mate choice. This progress has been  
661 facilitated by the integration of different fields, in particular between behavioural ecology and  
662 sensory ecology. However, our understanding of the consequences of these changes for populations  
663 and communities has remained poor. A larger effort should be made towards revealing the  
664 consequences of altered mate-choice systems at higher ecological levels than the individual.

665 We also need to develop our ability to predict which mate-choice systems will be affected by  
666 human activities, and which environmental changes will have the most damaging effects. These are  
667 challenging aims as we still have a poor understanding of why the strength of sexual selection  
668 varies among species in their natural habitat. Yet, the knowledge is of high importance in  
669 conservation and management practices.

670 Another understudied topic is the ability of species to adjust their mate-choice system to human-  
671 induced environmental changes through phenotypic plasticity and genetic changes. Questions that  
672 need to be addressed are: (1) when is plasticity enough and when are genetic changes needed, (2)  
673 how do the two processes interact, and (3) which factors influence the processes? In particular, the  
674 influence of the evolutionary history of the species and the factors that prevent or slow down  
675 genetic adaptation need to be addressed.

676 On a related topic, an unexplored field is the influence of altered mate-choice systems on eco-  
677 evolutionary dynamics. Mate-choice systems influence both ecological and evolutionary processes,  
678 but the impact on the interaction between them has rarely been considered. Yet, such effects are  
679 expected. For instance, declining population size because of reduced mate encounter rate can cause

680 the decline of predator populations (ecological effect), which, in turn, can decrease the cost of  
681 conspicuous sexually selected ornaments and, hence, allow for their evolution. This can, in turn,  
682 promote the growth of the population, resulting in further changes to the predator population, etc.  
683 Eco-evolutionary dynamics ultimately determine the long-term influence of human-induced  
684 environmental changes on populations and, hence, should be considered in studies on the effects of  
685 human activities on populations and communities (Hendry, 2017).

686 Another poorly studied topic is the impact of sexual conflict on mate-choice systems in changing  
687 environments. A recent study suggests that its relative importance could decrease when populations  
688 become maladapted to local conditions (Long *et al.*, 2012). However, how the absolute effect  
689 changes is unknown, as well as the pattern among species. Progress is hampered by our poor  
690 knowledge of the preponderance of sexual conflict in nature and the degree to which it reduces the  
691 viability of populations in terms of growth rate.

692 Finally, more attention needs to be directed to the influence of interactions among multiple  
693 environmental changes on mate-choice systems. Species are increasingly exposed to multiple  
694 disturbances, such as altered habitat structure, increased noise levels, and chemical pollution. How  
695 these multiple disturbances interact and affect mate attraction and mate choice is poorly known.

696 Interactions could result in unexpected, novel effects that are not predicted based on single effects,  
697 or they could magnify the impact of single effects. For instance, habitat destruction that increases  
698 male density in remaining habitats could increase the mating success of aggressive males with poor  
699 parenting ability, while simultaneous exposure to chemical pollution could reduce male  
700 aggressiveness. Predicting the ultimate impact on parenting ability and offspring production can be  
701 difficult under such conditions.

702

## 703 **IX. CONCLUSIONS**

704 (1) Human-induced environmental changes can alter mate-choice processes through effects on: (1)  
705 the expression and reliability of the traits assessed by mate choosers; (2) the transmission of  
706 information about courtiers to choosers; (3) the ability of choosers to receive and process the  
707 information; and (4) the mate preferences of choosers and their ability to execute mate choice.

708 (2) Changes in mate attraction and mate choice can, in turn, alter individual fitness – the number  
709 and quality of offspring produced – and, hence, impinge on population dynamics. This can, in turn,  
710 alter species interactions and, thus, the composition of the community. However, little attention has  
711 so far been paid to these effects, although mate choice is an important fitness determinant that  
712 influences the characteristics, viability and evolution of populations.

713 (3) Individuals may respond to changes in the mate-choice process by plastically altering their  
714 traits. Such responses can be adaptive or maladaptive, depending on the evolutionary history of the  
715 population and existing reaction norms. Evolutionary (genetic) changes may arise across  
716 generations and alter the traits, but how such changes to mate-choice systems influence population  
717 viability is poorly known, as both positive and negative effects are plausible.

718 (4) The impact of mate choice and sexual selection on population viability in changing  
719 environments is context dependent, with both positive and negative effects possible. Our ability to  
720 discern the ultimate impact is currently hampered by our poor knowledge of the adaptive value of  
721 mate-choice systems under natural, undisturbed conditions.

722

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1043 **Figure legends**

1044

1045 **Fig. 1.** The components of mate-choice systems and the factors that can influence them. During the  
1046 first stage of the mate-choice process – the expression of cues assessed by choosers – changes in  
1047 extrinsic factors and intrinsic properties of individuals can disrupt the correlation between cues and  
1048 mate quality, i.e. cue reliability. During the second stage - the transmission of information from the  
1049 assessed individual to choosers – changes in environmental conditions can alter the efficacy of  
1050 transmission. During the third stage, the reception and processing of the information can be altered  
1051 by environmental change. During the fourth stage (which is also taking place within the mate  
1052 chooser), mate preferences and the ability of choosers to exert choice can be affected. All these  
1053 alterations can influence the final mate choice.

1054

1055 **Fig. 2.** Adaptive and maladaptive alterations of sexually selected signals in response to  
1056 environmental change. In an undisturbed environment, the allocation of resources between naturally  
1057 selected traits and sexually selected signals may be adaptive and maximises fitness. If resources  
1058 decrease (A), the adaptive response could be to reduce investment into the signals to ensure enough  
1059 resources for naturally selected traits, which determine survival, growth and fecundity. Individuals  
1060 that continue to invest heavily in sexually selected signals will then respond maladaptively and  
1061 suffer fitness losses. If the value of the sexually selected signals decreases (B), for instance because  
1062 of poor signal transmission, the adaptive response could be to reduce investment into the signals in  
1063 favour of naturally selected traits. Maintaining high investment into the signals could then decrease  
1064 fitness.

1065

1066 **Fig. 3.** The relationship between signal expression and mate quality. (A) Signals are reliable when  
1067 they reflect mate quality. Environmental change may reduce reliability by (B) weakening the

1068 correlation between the signal and mate quality, (C) reducing the variation among individuals in  
1069 signal expression (or *vice versa*, reducing the variation among individuals in quality), or (D)  
1070 eliminating the correlation by increasing random variation in signal expression.

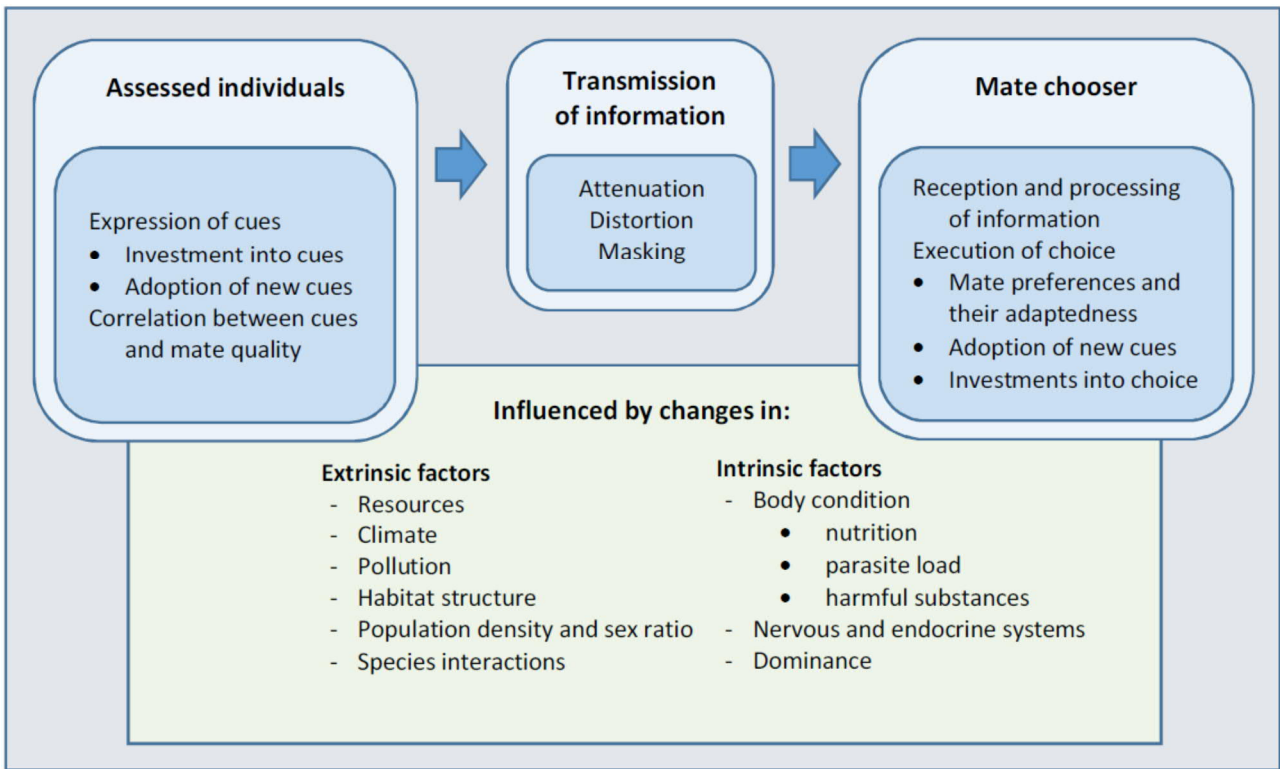
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1072 **Fig. 4.** Altered mate-choice systems can influence population dynamics. Increased costs of mate  
1073 attraction and sampling in a changing environment can increase adult mortality and reduce the  
1074 number of individuals attempting to reproduce. The number of individuals reproducing can be  
1075 further reduced by lowered mate encounter rate or altered mate choice. In addition, the quality of  
1076 the reproducing individuals can decline through changes in mate preferences and mate choice.  
1077 Combined, changes in the number and quality of individuals reproducing can alter the number and  
1078 viability of offspring produced.

1079

1080 **Fig. 5.** The rescue of mate-choice systems after environmental change. In an undisturbed  
1081 environment, selection has favoured the evolution of traits that increase mating success under the  
1082 prevailing conditions. A change in the environment reduces the fitness value of the traits. Plastic  
1083 alterations of the traits may quickly improve their fitness values, which may ensure population  
1084 persistence. This can, in turn, allow evolution to gradually improve the adaptive value of the traits.  
1085 Thus, the combination of plastic responses and genetic changes (evolution) can restore the fitness  
1086 benefit of mate choice.

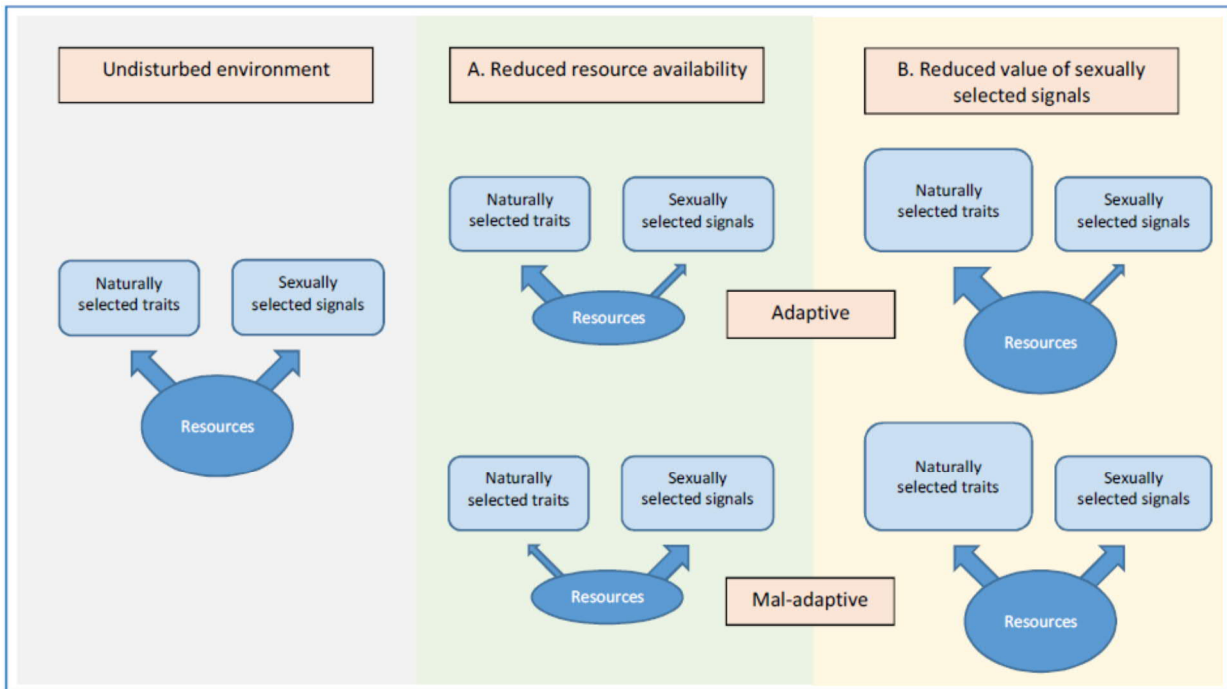
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1090 Fig 1

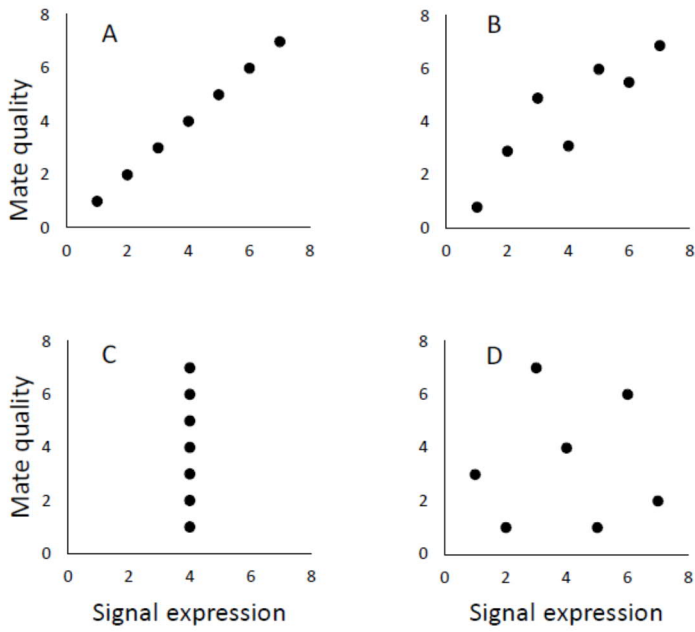
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1093 Fig 2

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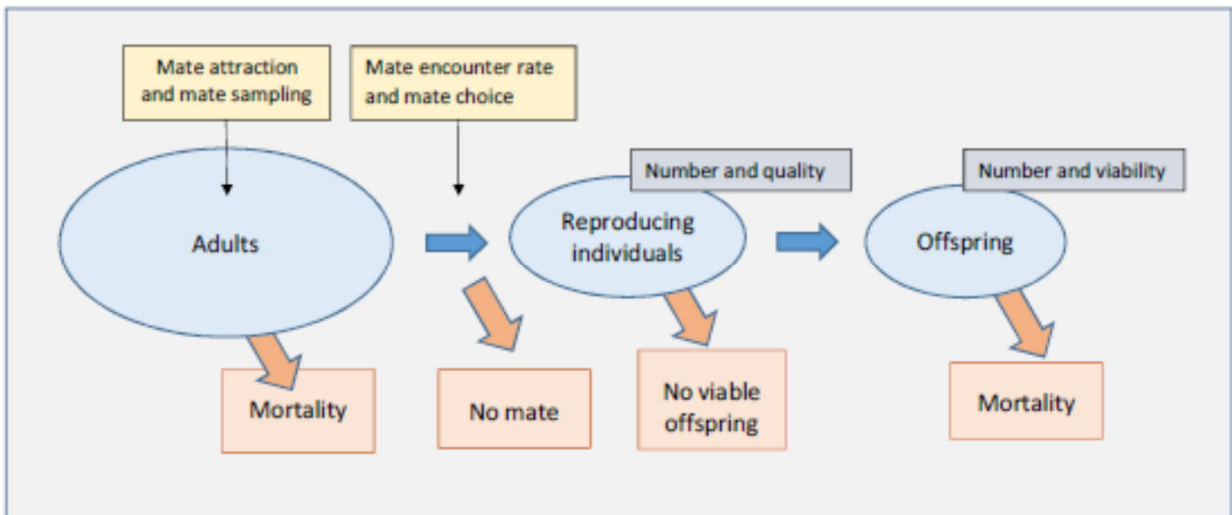


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1096 Fig 3

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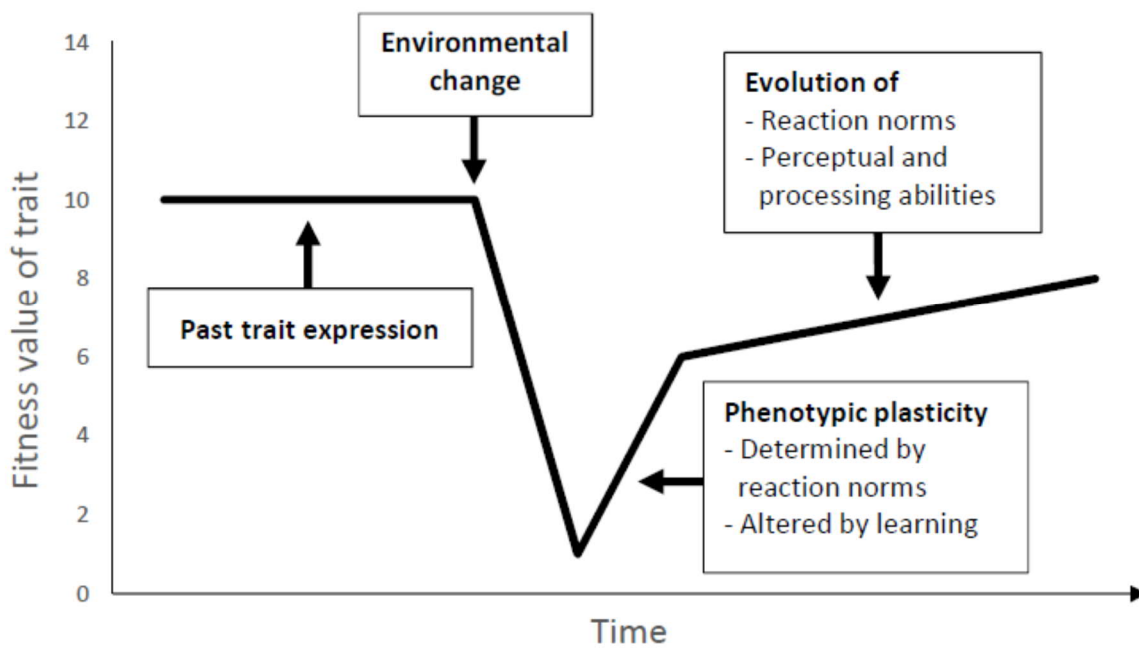
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1100 Fig 4

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1104 Fig 5